

Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panamá

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Abstract

In 1983, *Diadema antillarum* suffered mass mortality throughout the Caribbean Sea and the western Atlantic Ocean. I followed the dynamics of populations at the San Blas Islands, Panamá from April 1983 to November 1987. Density measurements indicate that populations of *D. antillarum* have not recovered from the die-offs that killed nearly 97% of the individuals. There was recruitment to the 1 to 1.5 cm class immediately after the mass mortality, but there has been little additional influx of juveniles since then. The low number of observable juveniles could not be attributed to elevated rates of predation on very small individuals. Rates of recruitment did not differ between reefs with artificially increased densities of *D. antillarum* and reefs kept free of sea urchins; thus, the lack of recruitment did not arise from absence of adults that could provide settlement cues to the larvae or protection to newly settled juveniles. Other species of sea urchins did not show a clear pattern of increase after the demise of *D. antillarum*. Therefore, interspecific competition directed towards *D. antillarum* juveniles did not increase after the mass mortality. Two reefs where *Echinometra viridis*, *Eucidaris tribuloides* and *Lytechinus williamsi* were removed showed no significant differences in recruitment of *D. antillarum* relative to two reefs where these species were allowed to remain at their natural densities. Resident *D. antillarum* after the mass mortality produced gametes with the same per capita intensity and lunar synchrony as before the mass mortality. However, it is possible that the probability of fertilization of their gametes decreased because of low population density. The most likely explanation for lack of recruitment is that the reduced numbers of reproducing adults at Panamá and upstream locations resulted in levels of larval supply that were inadequate to sustain recruitment on Panamanian reefs.

Introduction

Between January 1983 and February 1984, *Diadema antillarum* suffered mass mortality that began at Panamá and spread to the entire Caribbean Sea and the western Atlantic Ocean (Lessios et al. 1984b). The reduction in population density was recorded in Panamá (Lessios et al. 1984a), Jamaica (Hughes et al. 1985, Liddell and Ohlhorst 1986), Curaçao (Bak et al. 1984), Barbados (Hunte et al. 1986), St. John (Levitan in press, a), and St. Croix (Carpenter 1988); in all localities, 85 to 100% of *D. antillarum* on each reef perished. Qualitative observations indicate that populations in other parts of the Caribbean Sea suffered a similar fate (Lessios et al. 1984b). Before the mass mortality, *D. antillarum* affected the composition of algal (Carpenter 1981, 1986, Sammarco 1982a, b), coral (Bak and van Eys 1975, Sammarco 1980, 1982a), echinoid (Williams 1981), and fish (Williams 1980, 1981, Sammarco and Williams 1982, Hay and Taylor 1985) communities and the carbonate balance of the reef (Stearn and Scoffin 1977, Scoffin et al. 1980). Thus, its population dynamics after the mass mortality are of interest not only as a case study of the long-term effects of a severe population perturbation on a previously abundant species, but also as an investigation of a factor potentially important for the composition of coral reef communities in general. Here, I document the dynamics of Panamanian populations of *D. antillarum* for approximately five years following the mass mortality.

Materials and methods

Population density

The study site and the methods of assessment of population density of *Diadema antillarum* have been described in detail by Lessios et al. (1984a). Permanent quadrats had been established on eight reefs at the San Blas Islands off the Caribbean coast of Panamá before the 1983 mass mor-

tality. Three of these reefs (Vieja, Aguadargana, House) are in the Punta San Blas area, and five (Cayo Gallo, Open Coconut, East End, Panamá Flag, Chichime) in the Cayos Limones, approximately 7 km away. On six reefs, single 5×5 m quadrats were established. On two reefs, Aguadargana and House, three 1×1 m quadrats per reef were placed a few meters away from each other. All quadrat locations were in depths less than 6 m, the zone of highest abundance of *D. antillarum*. These quadrats, monitored from 1 May 1983 to 15 October 1983 to assess the magnitude of mass mortality (Lessios et al. 1984 a), were also examined in approximately bimonthly intervals until November 1987. All individuals of *D. antillarum* inside the quadrats were counted and measured. Individuals of other species of sea urchins were counted in the same quadrats after August 1983 in the Cayos Limones and after October 1983 at Vieja. On Vieja reef, the markings for the three original quadrats were lost in June 1983, and a new 5×5 m quadrat was set up. Mass mortality reached the Punta San Blas area in early April 1983 (Lessios et al. 1984 b), but started affecting the monitored reefs shortly before 1 May. At Cayos Limones, the die-offs started at the end of May 1983. Thus, data from quadrats on seven reefs provide continuous estimates of population size from the premortality state to the end of November 1987.

In addition to the quadrats, yearly population censuses of *Diadema antillarum* were conducted along transects on 11 reefs for which similar data had been gathered between 1980 and 1983. Before 1983, five to ten transects were haphazardly placed on each reef (see Lessios et al. 1984 a). After the 1983 mortality, ten transects per reef were laid down in the same manner. Each transect was 1.8 m wide, started at the shallowest point of the reef where *D. antillarum* were encountered before 1983, and extended to a depth of 17 m (or to the base of the reef if shallower than 17 m). Dates of transect surveys prior to 1983 are given in Lessios et al. (1984 a). After 1983 they were always performed between May and August of each year.

To see if fluctuations in populations of other species of sea urchins were correlated with changes in density of *Diadema antillarum*, I also conducted censuses of all echinoids on House Reef in habitats for which similar data had been gathered before the mass mortality (see Lessios et al. 1984 a). Five to ten transects, each 1.8 m wide, stretched from the shallowest point of each habitat to the habitat end or (in sea-grass beds) to a distance of 30 m. These censuses were done between May and August once a year between 1983 and 1987 except for 1984. In 1983, data were gathered in August, four months after the mass mortality of *D. antillarum*.

Reproduction

Annual reproductive periodicity of *Diadema antillarum* in Panamá had been studied in 1976–1977 (Lessios 1981) and lunar reproductive periodicity in 1982 (Lessios 1984). To see if reproduction was affected by the severe reduction in

population density, a new study was conducted in 1984, one year after the die-offs. Samples used in this study were collected at Vieja reef every third day from 24 August to 17 October 1984. The methods were the same as those used previously (Lessios 1984, 1985). Twenty adult *D. antillarum* per sampling day were injected with 5 ml of 0.5 M KCl solution; the percent of individuals that spawned copiously was used as an index of the reproductive state of the population.

Recruitment

The following observations and experimental manipulations were begun in 1983, after the demise of *Diadema antillarum*.

In order to study natural recruitment of *Diadema antillarum* more extensively than the 25 m² quadrats permitted, a permanent quadrat, 50 m on each side, was established on 10 November 1983 between House Reef and Nalunega (see Lessios et al. 1984 a for map). This quadrat was located in an area where in years previous to the mass mortality a large number of juvenile *D. antillarum* had been noted. One hundred *D. antillarum* with horizontal test diameters smaller than 1.5 cm had been collected in this area in four man-hours of searching on 11 December 1982. The sea floor in this area lies at a depth of 0.5 to 2.5 m and consists of sand, small live and dead corals, and sea grass. This substratum allows searches for juveniles to be conducted without destruction of the habitat. The 2500 m² quadrat was searched every two weeks from 10 November 1983 to 3 September 1986, and at more irregular intervals thereafter. Every *D. antillarum* located inside the quadrat was measured and then removed to ensure that individuals found subsequently had arrived in the time between censuses.

Effects of predation

To determine what effects predation upon *Diadema antillarum* juveniles might have on observed rate of recruitment, 120 hollow ceramic blocks, each 40×40×10 cm, were used. Three hollow areas, 40×10×8 cm each, with openings on the 40×10 cm side, existed in every block. Forty blocks were placed in each of three shallow areas in the vicinity of the 2500 m² quadrat with their openings facing in directions that alternated by 90 degrees. One set was located in a sea grass bed at a depth of 1.5 m, a second set on the reef flat at a depth of 0.5 m, and a third at the reef crest next to the reef slope at a depth of 1 m. The openings of 20 randomly chosen blocks in each set were covered by 1 cm-mesh hardware cloth to prevent fish, crabs, lobsters, and other potential macropredators from entering the hollow areas. The blocks were examined every two weeks from 28 April 1984 to 17 August 1986. All species of sea urchins residing in the holes were removed

and measured. The number of sea urchins less than 10 mm in horizontal test diameter found in each two-week interval was used as an index of recruitment.

Effects of prior echinoid residents

To determine the effects of adult *Diadema antillarum* on the rate of recruitment and to assess the possibility of competitive exclusion of newly metamorphosed *D. antillarum* by other sea urchins, the following treatments were initiated. In one patch reef, Omyra (designated as Porvenir 18 in Robertson's 1987 map), which measured approximately 24 × 17 m, all species of echinoids were removed. In another reef, Greek (on the west side of Porvenir 20 in Robertson's 1987 map), with approximate dimensions of 16 m × 8 m, surviving *D. antillarum* were permitted to stay, while all individuals of other echinoid species were removed. In December 1983, *D. antillarum*, 3.5 to 5.8 cm in horizontal diameter, were collected from surrounding reefs and added to Greek reef to bring the population density up to one individual per m². Densities close to this value were maintained thereafter by occasional additions of adults. A third, larger (70 × 32 m) reef (Deep 26) was divided in two parts with a hardware cloth fence: in one half (Deep 26E) the few surviving *D. antillarum* were removed; in the other half (Deep 26C) individuals of all echinoid species were permitted to exist. In July 1984, 1500 adult *D. antillarum* were added to Deep 26 C to produce a density of ca. 1 m². This density was maintained by occasional additions of new individuals.

In each treatment (except Deep 26 E), five permanent transects, composed of 1 m² quadrats jointed end-to-end were established. These transects were equally spaced, and traversed each reef from one end to the other, or to a distance of 17 m where the reef was wider. On Deep 26 E, only four transects were established. All transects were monitored approximately every two weeks from September 1983 (October 1983 at Greek) to June 1984, every month from July 1984 to August 1986, and at more irregular intervals thereafter (see Fig. 11). Censuses in all reefs were conducted within 3 d of each other. The order in which reefs were sampled varied from one month to the next. Although this procedure caused slight variations in sampling interval at each reef, it was adapted to avoid the possibility of introducing artificial variation in recruitment between reefs arising from the lunar spawning patterns of *Diadema antillarum* (Lessios 1984). Juvenile sea urchins with horizontal test diameters less than 1.5 cm were measured with vernier calipers; adults were counted. Individuals with tests measuring as little as 3 mm could occasionally be located within the quadrats, but multiple samplings of the same quadrats by different persons showed that only individuals with test diameters larger than 10 mm could be located reliably without destruction of the habitat. Recruiting individuals of species excluded from the treatment were removed both within and without the transects.

Echinometra viridis was the most abundant sea urchin on the study reefs, but individuals of *Eucidaris tribuloides*,

Lytechinus williamsi and *Tripneustes ventricosus* were also present. Separate data were taken for these species, but in the experimental treatments they were removed along with *Echinometra viridis*. Mean densities (averaged over transects) of *E. viridis* during the study period fluctuated between 10 and 21 individuals m⁻² at Deep 26 C and between 5 and 10 individuals m⁻² at Deep 26 E, the two reefs in which they were not removed. The corresponding values for the next most abundant species, *Eucidaris tribuloides*, were 0.20 to 0.95 individuals m⁻² at Deep 26 C and 0.12 to 0.47 individuals m⁻² at Deep 26 E, while *L. williamsi* and *T. ventricosus* were rarely encountered.

Results

Population density

The quadrats in both the Punta San Blas area (Fig. 1) and in the Cayos Limones (Fig. 2) show that *Diadema antillarum* populations did not recover in the 4½ yr following the mass mortality. A few individuals persisted in the quadrats at Vieja, Aguadargana, East End, Panamá Flag, and Chichime, but even these had disappeared by the end of 1983. During the next 4 yr only an occasional *D. antillarum* was found, but the quadrats as a whole indicate no recovery of the species in the San Blas area. Since the permanent quadrats were located in the zone where aggregation occurred before the mass mortality, one can conclude that *D. antillarum* was rare or absent on these reefs, with one caveat: repeated measurements in the same quadrats eliminate variation due to patchy distribution, but could give a misleading picture of population density if the echinoids emigrated from the sampled area. That this is not the case is indicated by data from transects spanning all

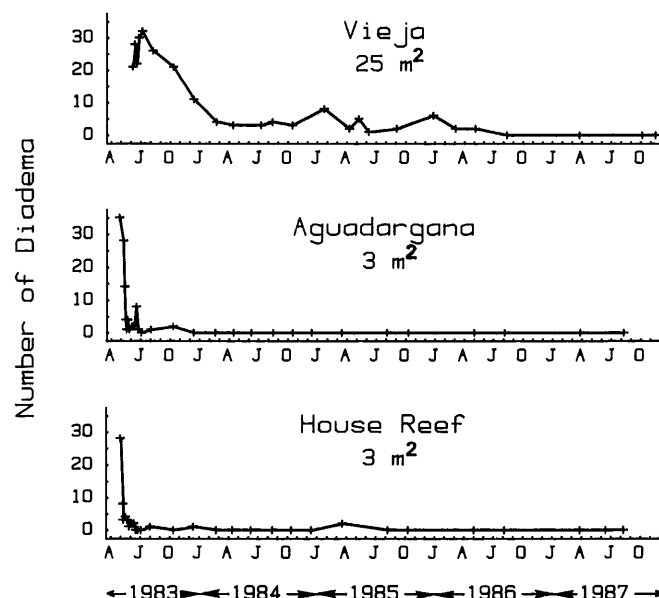


Fig. 1. *Diadema antillarum*. Numbers over time in each quadrat in Punta San Blas area, April 1983–November 1987

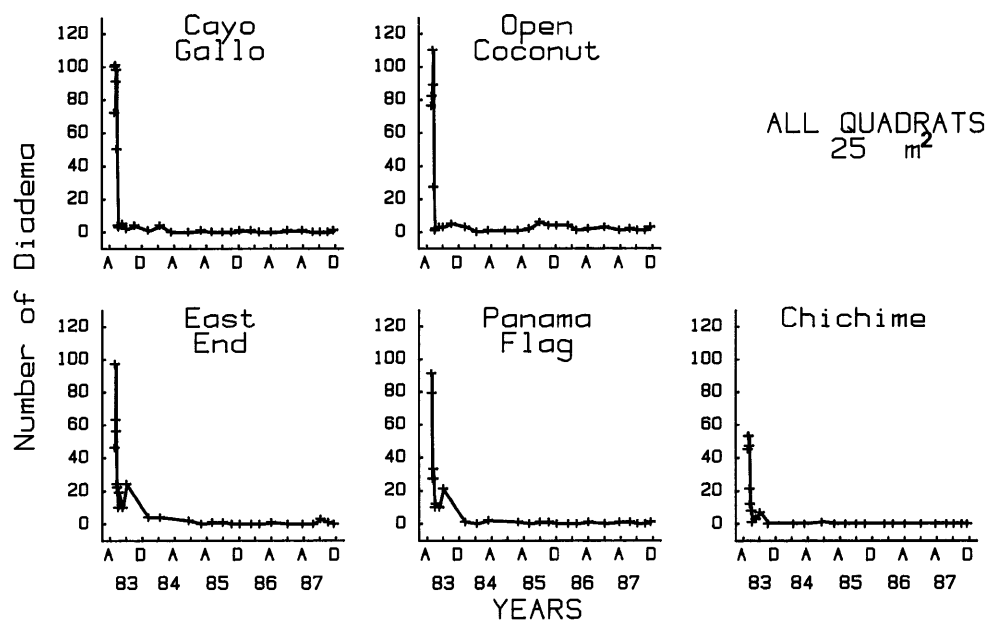


Fig. 2. *Diadema antillarum*. Numbers over time in each quadrat in Cayos Limones, April 1983–November 1987

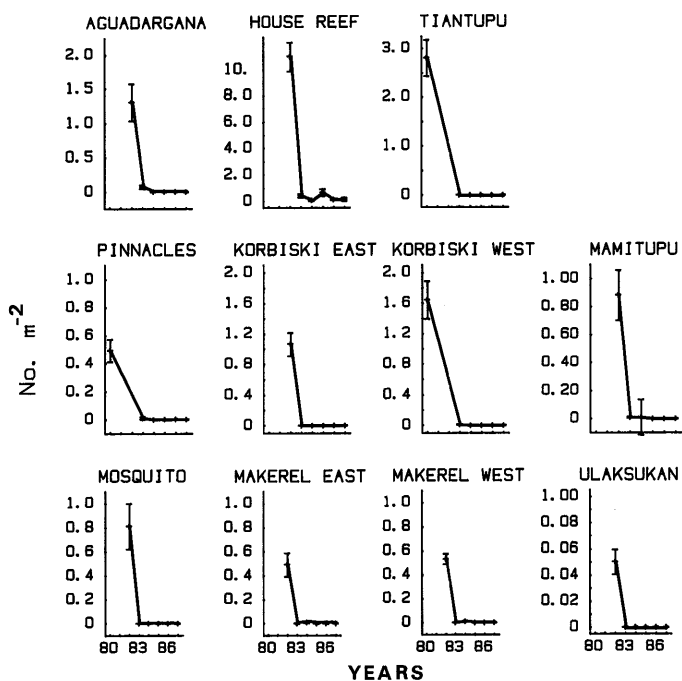


Fig. 3. *Diadema antillarum*. Means \pm standard errors of population density determined by transects at 11 reefs in Punta San Blas area. Lack of standard error bars indicates that no transect on that reef in that sampling interval contained a live *D. antillarum*. Note differences between reefs in scales of y-axes

depths at which *D. antillarum* could be found before the mass mortality (Fig. 3). They also indicate that *D. antillarum* has not recovered since the epidemic. When data from quadrats and transects are taken into account, it is clear that no recovery of *D. antillarum* took place in the San Blas Islands from May 1983 to November 1987.

Recruitment

Although the numbers of *Diadema antillarum* in the quadrats were too small to permit size-frequency analyses, potential recruitment to larger sizes can be represented by the numbers of small *D. antillarum* found over time. In both the Punta San Blas region (Fig. 4) and at the Cayos Limones (Fig. 5), some recruitment of juveniles occurred soon after the mass mortality. However, this recruitment soon ceased. Densities of individuals less than 1.5 cm in diameter were not higher than 0.08 m^{-2} after October 1983. As can be deduced from the total number of *D. antillarum* present in the same quadrats (Figs. 1 and 2), juveniles that were initially present did not grow into larger size classes, but instead died or emigrated.

Data from the 2500 m^2 quadrat at House reef indicate that disappearance of young *Diadema antillarum* from other quadrats is not an artifact of emigration, but the result of lack of recruitment. In this quadrat, so large that emigration of small individuals from the center would have been very unlikely in the two-week interval between censuses, numbers of juveniles were also very low (Fig. 6). Some recruitment occurred from November 1983 to January 1984. No more than two juveniles (a density of $0.0008 \text{ juveniles m}^{-2}$) were found inside this quadrat in any two-week sample after 9 January 1984. No individuals were present between 17 March 1985 and 27 March 1987. Since all *D. antillarum* found within this quadrat were removed, it can be argued that rate of larval settlement or survivorship of newly metamorphosed sea urchins may have been affected by the absence of conspecific residents. However, results from reefs where adult *D. antillarum* were added indicate that this has not been the cause of the low rate of recruitment (see p. 523).

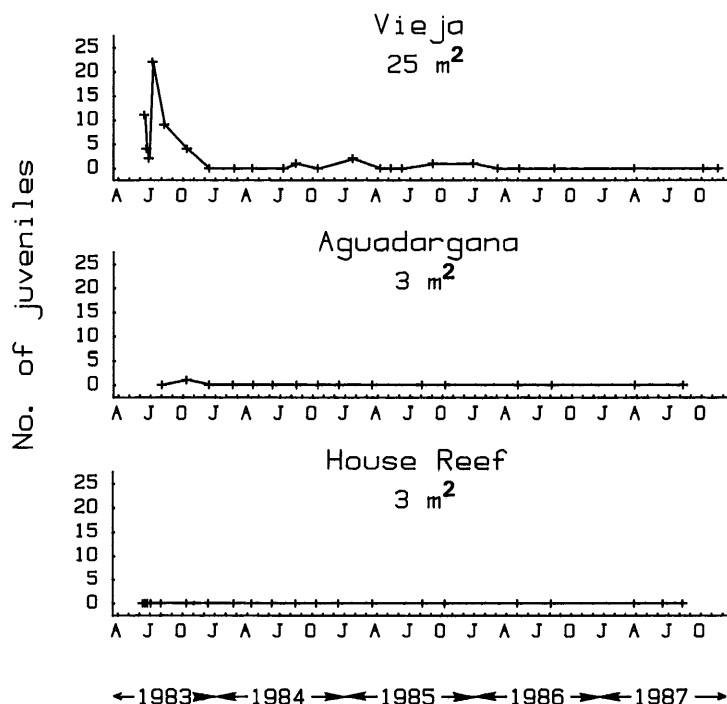


Fig. 4. *Diadema antillarum*. Number of individuals measuring < 1.5 cm in horizontal diameter over time in each quadrat in Punta San Blas area. Quadrats are same as those in Fig. 1

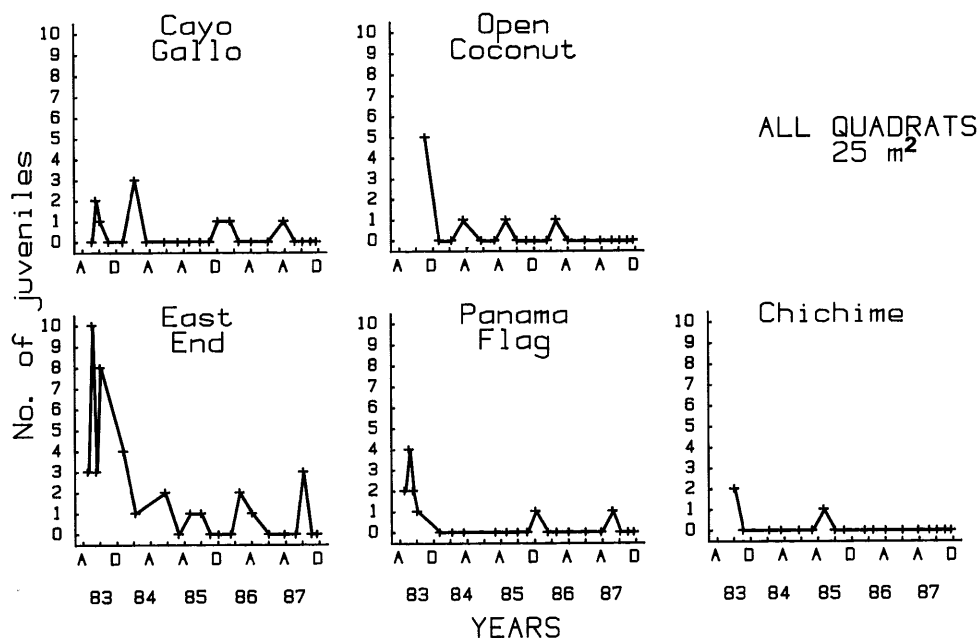


Fig. 5. *Diadema antillarum*. Numbers of individuals measuring < 1.5 cm in horizontal diameter over time in each quadrat in Cayos Limones. Quadrats are same as those in Fig. 2

The majority of *Diadema antillarum* at Vieja reef contained gonads full of gametes two days after new moon between 24 August and 17 October 1984 (Fig. 7), a time at which populations at this reef were at their minimum (Fig. 1). The percent of the population that responded to KCl injections in 1984 was about the same as in 1982. The lunar timing of reproduction in 1984 was no different than in years previous to the mass mortality (Lessios 1984). Lack of recruitment was not due to failure of adults to produce gametes.

Results from protected and unprotected blocks indicate that the low observed rate of recruitment was probably not due to predation on newly metamorphosed individuals. One species, *Echinometra lucunter*, recruited to the reef flat in appreciable numbers (Table 1). Numbers of juveniles of this species were significantly higher in blocks where protection from predators was provided ($\chi^2 = 43.6, p < 0.001$). *Diadema antillarum* and some other species of sea urchins did not recruit to the blocks, whether their entrances were covered with hardware cloth or not. In

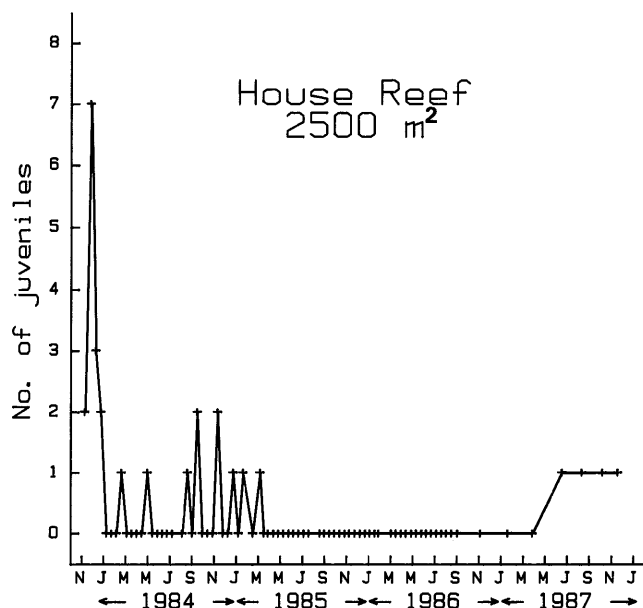


Fig. 6. *Diadema antillarum*. Numbers of individuals measuring less than 1.5 cm in horizontal diameter in a 2500 m² quadrat from which they were removed every 2 wk

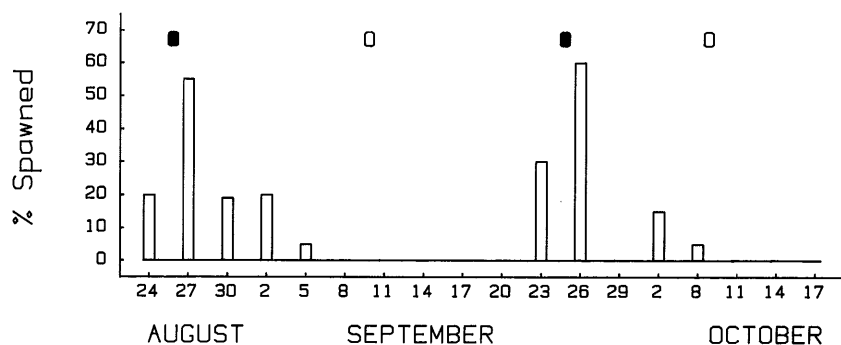


Fig. 7. *Diadema antillarum*. Percent spawning copiously in response to KCl solution injections over time; 20 individuals were injected every third day. Phases of moon are shown at top: ■, new moon; □, full moon

Table 1. Recruitment of sea urchins to ceramic blocks at San Blas Islands. Total numbers of individuals less than 1 cm in horizontal test diameter of each species found in the hollow areas of 40×40×10 cm ceramic blocks in each of three habitats, between 28 April 1984 and 17 August 1986. Forty blocks were present at each habitat, half with openings uncovered, half with openings protected with 1 cm-mesh hardware cloth. All blocks were examined every 15 d

Habitat	<i>Diadema antillarum</i>	<i>Lytechinus variegatus</i>	<i>Lytechinus williamsi</i>	<i>Echinometra viridis</i>	<i>Echinometra lucunter</i>	<i>Eucidaris tribuloides</i>
Reef crest						
Uncovered	1	1	0	1	3	2
Covered	0	2	0	2	2	2
Reef flat						
Uncovered	0	1	0	0	19	0
Covered	1	0	0	0	87	3
Sea-grass bed						
Uncovered	0	0	0	0	0	0
Covered	0	0	1	1	0	0
Total						
Uncovered	1	2	0	1	22	2
Covered	1	2	1	3	89	5

2½ yr, only two *D. antillarum* were found in the 120 blocks. Each arrived at a different time. Thus, protection from predators was important for *E. lucunter*, in which recruitment was substantial. Protection from predation did not increase the rate of recruitment in species which did not recruit to the blocks. Therefore, predation on small juveniles alone cannot account for the low observed rate of recruitment of *D. antillarum*.

Population densities of other species of sea urchins found in the quadrats after the mass mortality of *Diadema antillarum* are presented in Fig. 8. Only data for species with more than an occasional individual present are shown. No clear trend of a numerical increase over time by any species after the mass mortality is evident. Similarly, the annual surveys of all other echinoid species in three habitats at House Reef (Figs. 9 and 10) failed to show a sustained increase in density over 1982 levels. *Echinometra lucunter*, *Clypeaster rosaceus*, and *Lytechinus variegatus* increased in numbers at the reef flat, particularly in 1986, but the significant increase of *E. viridis* at the reef flat in 1983, which led Lessios et al. (1984a) to raise the possibility of release from competition by *D. antillarum*, was not sustained in the following years. Since density of *D. antillarum*

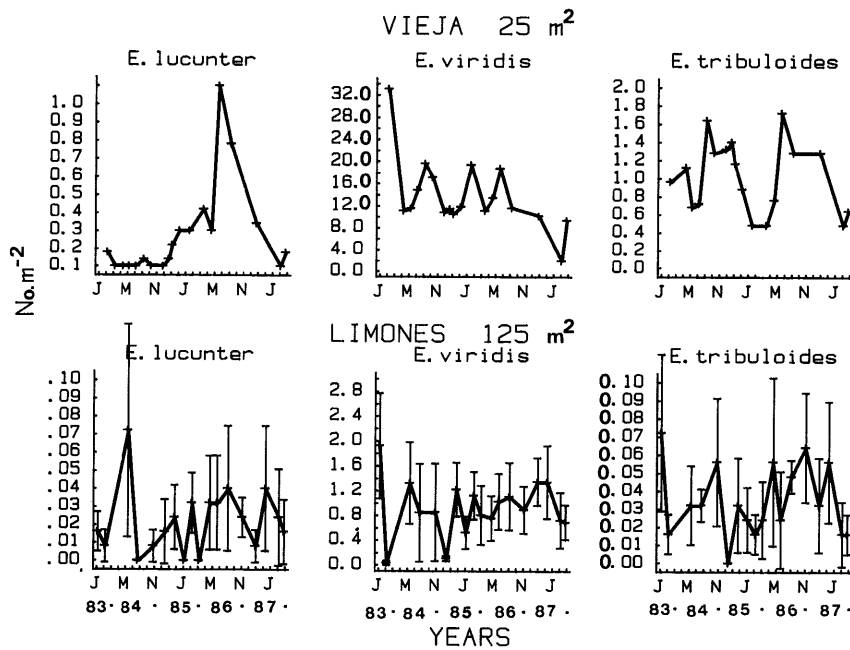


Fig. 8. *Echinometra lucunter*, *E. viridis*, and *Eucidaris tribuloides*. Density in quadrats at Vieja and at five locations at Cayos Limones. Same quadrats depicted in Figs. 1 and 2 were used for these measurements. For Cayos Limones, means \pm one standard error of values from the five quadrats are reported. Note differences between species in scales of y-axes

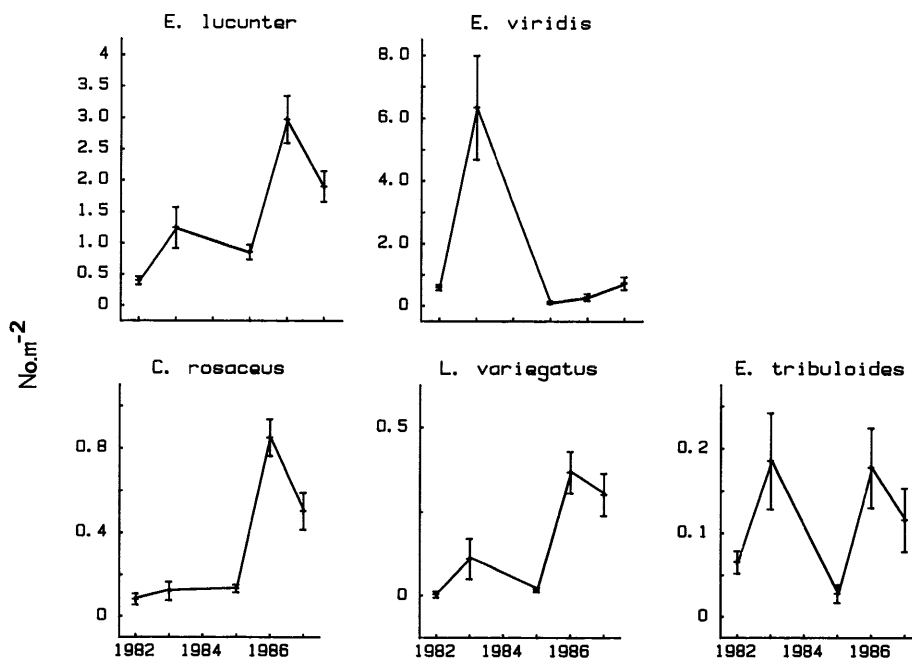


Fig. 9. *Echinometra lucunter*, *E. viridis*, *Clypeaster rosaceus*, *Lytechinus variegatus* and *Eucidaris tribuloides*. Means \pm standard errors over time of density at reef flat of House Reef. Note differences between species in scales of y-axes

at House Reef dropped in May 1983 and has remained low since then (Figs. 1 and 3), it is unlikely that any increases seen in 1986 are connected to the population collapse of this species. Thus, a negative correlation between population densities of adult *D. antillarum* and other species of sea urchins (that would have been expected had competitive release occurred) is not present. This makes it unlikely that competition could account for the low rate of recruitment by *D. antillarum*.

Data from the four reefs where densities of sea urchins were manipulated (Fig. 11) also indicate that recruitment has been very low. Numbers of *Diadema antillarum* recruits

per quadrat from each sampling period in Deep 26C, Deep 26E, Omyra and Greek reefs were compared in one-way hierarchical ANOVAs, with transects considered as subgroups of reefs. Only one comparison (for 18–19 January 1984) out of the 47 is significant at the 0.05 probability level, with Deep 26C having an average density of 0.05 juveniles per square meter and the other reefs having none. With 47 comparisons, two would appear to be significant at the 0.05 level due to chance alone. Thus, addition of adult *D. antillarum* to Deep 26C and Greek did not enhance recruitment relative to other reefs; nor did the absence of other sea urchins in Omyra and Greek increase

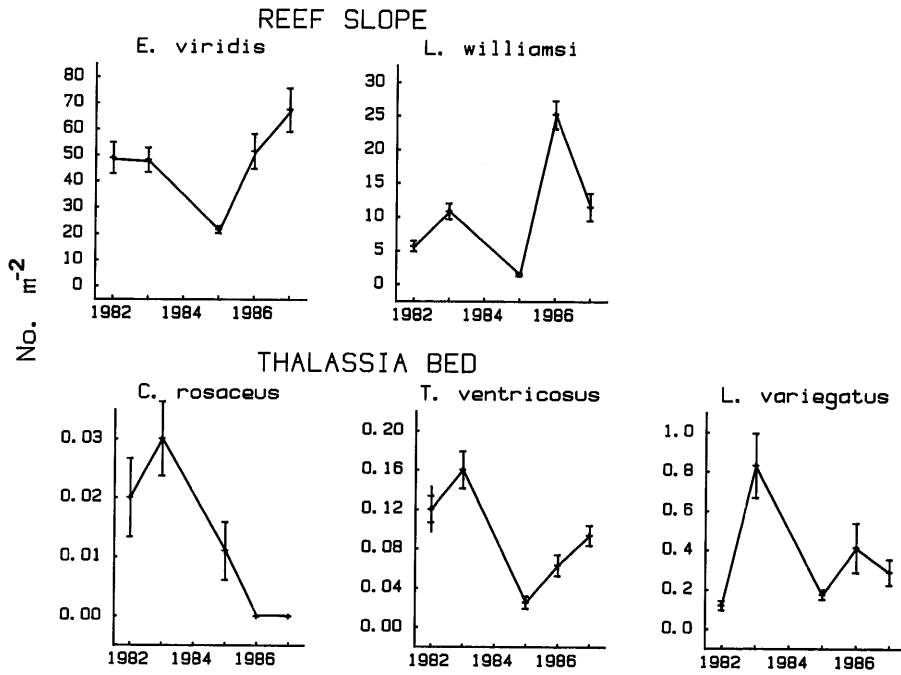


Fig. 10. *Echinometra viridis* and *Lytechinus williamsi* (reef slope) and *Clypeaster rosaceus*, *Tripneustes ventricosus* and *L. variegatus* (sea grass bed). Means \pm standard errors over time of densities at House Reef. Note differences between species in scales of y-axes

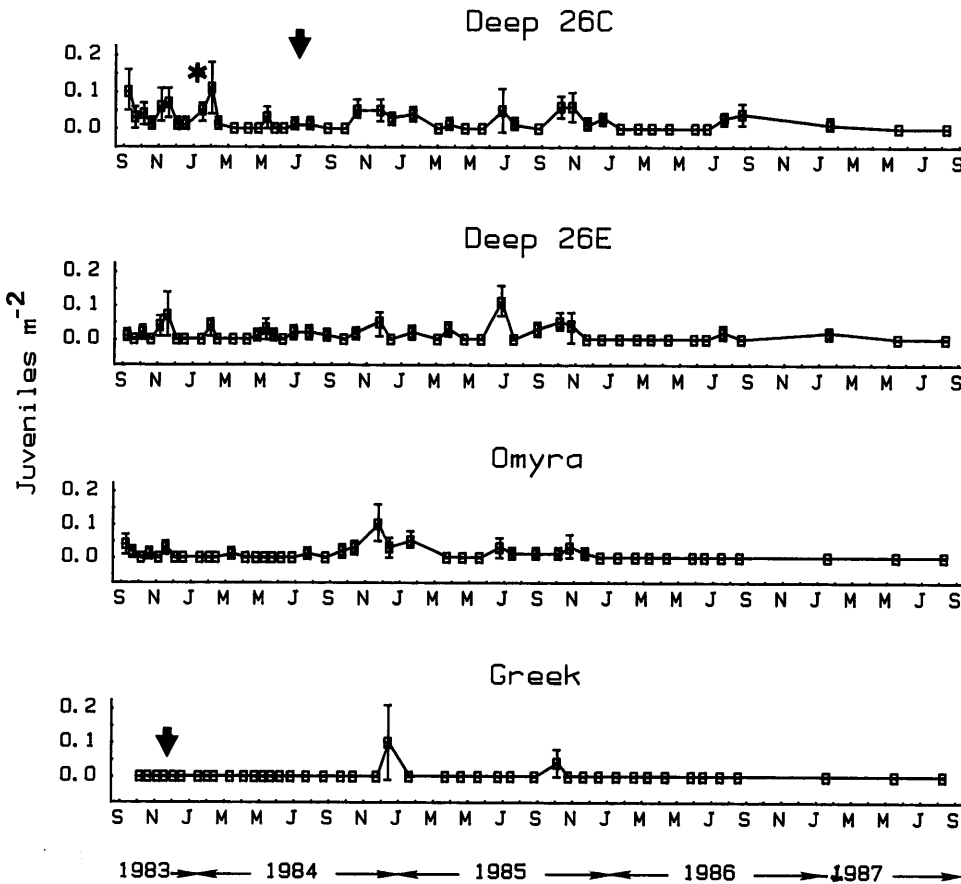


Fig. 11. *Diadema antillarum*. Means \pm standard errors over time of density of individuals measuring less than 1.5 cm in horizontal diameter at Deep 26C, Deep 26E, Omyra, and Greek reefs. Mean densities of five transects per reef were averaged, except for Deep 26E, in which four transects were used. Deep 26C had all naturally occurring echinoid species present, and *D. antillarum* added to a density of 1 per m²; Deep 26E had *D. antillarum* removed and all other echinoid species present; Omyra had all echinoids removed; Greek had all other echinoids removed, but *D. antillarum* added to a density of 1 per m². The asterisk in Deep 26C indicates the only nested ANOVA (quadrats nested within transects, transects nested within reefs) comparison of mean densities that is significant at $p < 0.05$. Arrows in Deep 26C and Greek indicate times of *D. antillarum* additions to maintain population densities close to 1 per m²

the rate of *D. antillarum* recruitment. When numbers of adult *D. antillarum* were augmented at Deep 26 in July 1984, rate of recruitment of juveniles did not increase. The few juveniles that settled at various times did not remain in the transects. Here, as in the Punta San Blas and Cayos Limones quadrats, the disappearance of juveniles was not due to growth out of the < 1.5 cm interval, but to mortality or emigration.

Discussion

Populations of *Diadema antillarum* in the San Blas Islands show no signs of recovery five years after the 1983 mass mortality. Indeed, they have declined to densities even lower than those attained immediately after the die-offs. Data from 17 reefs show that this lack of recovery is widespread. If these data were to be interpreted as precise estimates of population density in the entire San Blas Archipelago, one would conclude that *D. antillarum* has become extinct in this area. However, on a few reefs, not included in this study because no pre-mortality density data were available, a substantial number of *D. antillarum* can be found. Sometimes they aggregate at the reef crest at fairly high point-densities. Nevertheless, such reefs are rare.

Every quadrat and experimental treatment shows a very low rate of recruitment to the 1 to 1.5 cm size interval. Newly metamorphosed *Diadema antillarum* measure about 1 mm in horizontal diameter (Bak 1985). Growth-rate estimates for very young *D. antillarum* range from Bak's (1985) calculation of 4 mm per month, to Bauer's (1982) measurements of two laboratory-reared individuals that grew an average of 8 mm in the first month. By these estimates individuals 10 to 15 mm in diameter were 1.25 to 3.75 mo old. Hunte and Younglao (in press) found peak accumulation of individuals 10 to 15 mm in diameter 4 mo after spawning by adults in Barbados. *D. antillarum* of this size would be 2.5 mo old if recruits in Barbados come from larvae produced in the same area, and if the larval period lasts about 6 wk. Thus, up to 4 mo could elapse between the time adults in Panamá or other areas of the Caribbean spawn and the time new recruits can be located on the San Blas reefs. What factors operating during this 4 mo interval might account for the observed low rate of recruitment?

Lack of recruitment between 1983 and 1987 might be unrelated to the mass mortality. It could be argued that, like some temperate sea urchins (Ebert 1983, Pearse and Hines 1987) or temperate and tropical seastars (Birkeland 1982, Ebert 1983), *Diadema antillarum* may always display wide variations in recruitment success. The convergence of conditions necessary for peak recruitment may have not occurred in the five years spanned by this study. The possibility that low recruitment is unrelated to the mass mortality is low. Several authors studied size-frequency distributions of *D. antillarum* over time in years previous to the mass mortality. Lewis (1966) and Hawkins and Lewis (1982) in Barbados as well as Bauer (1976) in Florida discerned distinct small size-classes, and followed their

growth. That these studies lasted for a maximum of only 12 mo yet changed upon a recent recruitment event indicates that pre-mortality populations of *D. antillarum* used to receive a frequent influx of new recruits. Bak (1985), who followed recruitment on artificial substrata of *D. antillarum* 1 to 3 mm in diameter at Curaçao between April 1982 and December 1984, found that recruitment was high and predictable until it ceased completely five months after mass mortality affected this island. It is unlikely that this correlation is not the result of direct causal relationship between mass mortality and recruitment. The data from Panamá (Figs. 4–6) also show this pattern of recruitment immediately after the mass mortality and subsequent cessation of any discernible addition of juveniles to the population. It seems probable that recruitment of *D. antillarum* was a regular event before the mass mortality, and that the current lack of juveniles is connected with that event.

Is the paucity of juveniles of *Diadema antillarum* in the San Blas Islands after the mass mortality due to a low rate of zygote production, or to high mortality during the 4 mo period during which larvae and very small juveniles cannot be observed? Three hypotheses would involve inadequate zygote production:

(1) Mass mortality could have interfered with gonadal maturation of adults or reproductive synchrony of the populations. This hypothesis can be ruled out; *Diadema antillarum* in the San Blas Islands a year after the mass mortality spawned with the same intensity as a year before the event. Levitan (in press, b) also found peak reproductive activity of *D. antillarum* right after new moon at St. John between 1984 and 1987. Younglao and Hunte (in press) found that the annual reproductive cycle of *D. antillarum* at Barbados in 1985 was similar to those in 1962 and 1963 (Lewis 1966), and that lunar cycles in spawning existed. Although the lunar reproductive rhythm at Barbados had a peak 15 d out of phase with the rest of the Caribbean (Bauer 1976, Iliffe and Pearse 1982, Lessios 1984), this did not affect reproductive synchrony within the population. Thus, surviving *D. antillarum* are capable of producing gametes, and their gonads mature with a lunar rhythm. This pattern existed before 1983, and suggests that lack of recruitment is not the result of reproductive failure.

(2) Reduced population size could have decreased the probability of fertilization. Given the small radius around an adult male that sea urchin eggs can be fertilized (Pennington 1985), isolated individuals, even if spawning at the same time as the rest of the population, would produce few larvae. This hypothesis is credible. Before mass mortality, *Diadema antillarum* tended to be more aggregated during the spawning season (Bauer 1976), which could indicate that there was a premium in close proximity with conspecifics during spawning even when densities were high. Alternatively, reproductively active individuals may have been seeking the best spawning grounds, in which case aggregation was a passive by-product of a limited number of such sites. Whether passive or active, and whether enhanced during reproduction or not, aggregation after mass

mortality (Levitan in press, b) could mitigate the effects of small population size on rate of gamete fertilization. However, in most San Blas reefs, population size has been reduced to such an extent that individuals are separated by tens of meters. Even if they did form reproductive aggregations, such aggregations would consist of fewer individuals, thus resulting in lower probabilities of fertilization and lower rates of larval production per individual.

(3) The number of reproducing adults in Panamá and upstream regions could have been reduced to such an extent that the absolute number of larvae released into the water column is not sufficient to support recruitment at a level that can sustain a positive population growth. This hypothesis of inadequate larval supply, perhaps in combination with the possibility of reduced fertilization success, fits the existing data. It would explain why recruitment was present immediately after the mass mortality, while larvae released earlier by Panamanian populations were still in the water column and while populations of *Diadema antillarum* on the north coast of South America, upstream from Panamá, had not yet been devastated (Lessios et al. 1984b). It also agrees with Bak's (1985) findings from Curaçao. The hypothesis should not be interpreted literally as meaning that the number of settling larvae per resident adult – after mortality in the plankton takes its toll – has remained unaffected by the mass mortality. If this were true, and if the relationship between resident stock and recruitment were linear, populations should have remained constant at the level they reached after the initial spurt of recruitment. The hypothesis suggests that, given the spatial and temporal variability that probably exists in settlement, a minimum number of larvae are required in the water column in order to produce a finite probability of settlement and survival on a limited number of reefs. It seems that populations of *D. antillarum* at Panamá and upstream regions could not produce this minimum number of larvae between May 1983 and November 1988. In the absence of recruitment adequate to counteract adult mortality, populations have declined, further reducing the probability of production of new recruits.

Six hypotheses would involve mortality to explain lack of recruitment:

(1) Mortality during the larval stage could have increased after the mass mortality. We know nothing about processes affecting larval survivorship in *Diadema antillarum* either before or after the population collapse, but the continuation of recruitment after adult populations died indicates that the mass mortality agent, presumed to be a water-borne pathogen (Lessios et al. 1984a, b), did not affect larvae.

(2) Larvae might perish without settling on Panamanian reefs because they do not detect the presence of adults, which in some echinoids are known to induce larvae to settle from the plankton (Highsmith 1982), or because they do not find adequate settlement sites prepared by the activities of adult *Diadema antillarum* (Bak 1985). That recruitment on Deep 26C and Greek reefs, with densities of *D. antillarum* artificially increased to pre-mortality

levels, was not significantly higher than on Deep 26E and Omyra which contained no *D. antillarum* at all, indicates that lack of settlement stimuli provided by adults is not a sufficient explanation for the absence of recruitment.

(3) The presumed pathogen that caused the mass mortality may still be present in Panamanian waters, and it may be killing newly metamorphosed individuals. This hypothesis is unlikely. It is virtually certain that the agent of mortality stopped operating on each reef after it killed most *Diadema antillarum*. Otherwise, *D. antillarum* should not persist in the area, and the echinoids added to Deep 26C and Greek reefs should have died. It could be argued that adults surviving in the San Blas are either resistant or immune to the pathogen, while juveniles are not, but this supposition is refuted by the numerical preponderance of juveniles immediately after the die-offs (Lessios et al. 1984a) and by a single recurrence of the presumed disease between November and December 1985. During this time, some individuals on various reefs showed symptoms similar to the ones present during the mass mortality (Bak et al. 1984, Lessios et al. 1984a, Hughes et al. 1985). This time the extent of the epidemic was very limited. Of 1930 *D. antillarum* individuals examined between 18 and 25 December 1985, only 11 (0.6%) showed symptoms of ill health. Despite constant observation of *D. antillarum* in the course of this and other studies, these symptoms were never noticed at any other time, indicating that the presumed pathogen was absent or inactive.

(4) The absence of adult *Diadema antillarum* may have resulted in lack of protection for juveniles, as has been hypothesized for other species of sea urchins (Tegner and Dayton 1977, 1981, Cameron and Schroeter 1980, Breen et al. 1985). Mortality due to lack of conspecific adults that would normally protect juveniles would not explain the low number of observed juveniles after 1983. Reefs where densities of *D. antillarum* were artificially increased showed no more recruitment than reefs where all *D. antillarum* were removed.

(5) Predators that prefer *Diadema antillarum* but are now subsisting mostly on other prey (Reinthal et al. 1984, Robertson 1987) may have retained their original population densities and feeding preferences, thus putting increased pressure on the few remaining adults and juveniles. This hypothesis cannot be discounted. An unusually large settlement of the known predator of *D. antillarum*, the queen triggerfish *Balistes vetula* in the San Blas during the early part of 1985 (Robertson 1987) might have further increased the risk of predation on any settling *D. antillarum*. However, results from protected and unprotected ceramic blocks show that the existence of refuges for juvenile *D. antillarum* did not increase recruitment. Although *D. antillarum* may not be prone to settling inside ceramic blocks, the general lack of recruitment on any other site would indicate absence of settlement as the most likely cause of the paucity of juveniles inside the blocks. Results from this experiment cannot rule out predation completely, because the 1 cm openings of the hardware cloth did not exclude micropredators that could feed on newly settled

D. antillarum. However, protected bricks did not permit the entrance of adult wrasses, such as *Thalassoma bifasciatum* and *Halichoeres bivittatus*, which appear to be one of the chief predators on juvenile *D. antillarum* (own unpublished observations). Before the mass mortality, caging of areas in sea-grass beds increased recruitment of *D. antillarum* considerably (Keller 1982), indicating that important predators can be excluded even with large-mesh cages. That the blocks placed in sea-grass beds had no recruits (Table 1), supports the conclusion that lack of settlement, rather than predation, is responsible for the results.

(6) Juvenile *Diadema antillarum* may have been excluded by adults of other species of sea urchins, released from competition with adults of *D. antillarum*. *Echinometra lucunter* and *E. viridis* display agonistic behavior towards other sea urchins that approach their crevice. They can often exclude intruders smaller than themselves (Shulman unpublished data). It is conceivable that these species could have an adverse effect on survivorship of juvenile *D. antillarum* by denying them access to crevices. Williams (1981) found that there was an inverse correlation between densities of *E. viridis* and *D. antillarum* in small-scale experimental manipulations. However, in the San Blas Islands, the abundance of *E. viridis* and other sea urchins did not show a steady increase from 1983 to 1987 as would have been expected if their populations had previously been regulated by competition with *D. antillarum*. This expected numerical response was also absent at Jamaica (Hughes et al. 1987). What is more, removal of other sea urchins from two reefs resulted in no significant increase of recruitment of *D. antillarum*, whether or not conspecific adults were present, which suggests that neither inter- nor intraspecific competition could account for lack of *D. antillarum* recruitment.

Thus, the lack of recruitment of *Diadema antillarum* in the San Blas Archipelago is most likely due to the lack of an adequate number of larvae in the water column. Processes that affect mortality of early life stages do not seem to be different under the present low population densities than when densities were high. They cannot by themselves account for the low influx of juveniles into the populations. Although these processes may have been important for *D. antillarum* when larval production was high, they obviously cannot act when few larvae exist.

The post-mortality population dynamics of *Diadema antillarum* in Panamá resemble dynamics of populations at Dominica, St. Lucia (Hunte and Younglao in press), Jamaica (Hughes et al. 1987) and at St. John (Levitan in press, a), but differ from those at Barbados (Hunte and Younglao in press). In the first four islands, little post-mortality recruitment of *D. antillarum* has occurred. In Barbados, however, there has been strong recruitment as of June 1985. In October 1985, populations of *D. antillarum* in three reefs averaged 37.7% of the density before the mass mortality. The dissimilarity between Barbados and the rest of the Caribbean may arise from the form of the relationship between stock and recruitment. More *D. antillarum* were present at Barbados after the mass mortality

than anywhere else. Average post-mortality population density of *D. antillarum* at Barbados (Hunte et al. 1986) was an order of magnitude higher than post-mortality densities on most reefs at Panamá (Lessios et al. 1984 a). Considering that the post-mortality density at Barbados is higher than densities in most Panamanian reefs before the die-offs (Lessios et al. 1984 a), it is possible that, as Hunte and Younglao concluded, local populations at Barbados produce enough larvae to restock local reefs. If so, the relationship between stock and recruitment may be non-linear, possibly because of the effects of population density on rate of fertilization.

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